Hybridization of the Brazilian *Papilio* (Pyrrhosticta) (Section V) with the North American *Papilio* (Pterourus) (Section III)

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Abstract. Male *Papilio* (*Pyrrhosticta*) *scamander* Boisd, from Campinas, Brazil were hand-paired to virgin *P.* (*Pterourus*) *glaucus* L. and *P.* (*Pterourus*) *palamedes* Drury females. Egg viability was less than 10% for two *P. glaucus* × *scamander* crosses and 18% for two *palamedes* × *scamander* crosses. *glaucus* × *scamander* larvae developed to pupation on sweetbay, tuliptree and cucumbertree (Magnoliaceae) and black cherry (Rosaceae) but died on redbay (Lauraceae). *P. palamedes* × *scamander* larvae developed to the last instar on redbay and camphortree (Lauraceae), but none pupated successfully. One female and 3 male *glaucus* × *scamander* adults emerged. Backcrosses were unsuccessful in producing viable eggs. Similarities of *P. scamander* adults, larvae and food plant use with the Mexican *P. garamus* Geyer are intriguing. Crosses of Brazilian *P.* (*Pyrrhosticta*) *cleotas* Gray with *P. glaucus* gave a higher egg fertility (68%) and the larvae fed well on *Talauma ovata* and *Michelia champaca* (Magnoliaceae), though none molted to the second instar. These results suggest a closer biological relationship between the five species mentioned than their current placement in two (sub) genera and four species groups would indicate.

Introduction

Of the 560+ species of Papilionidae (Munroe 1961, Hancock 1983, Collins and Morris 1985, Miller 1987), only 62 species are reported to use hosts from more than one plant family, and only 23 species use more than 3 food plant families (Scriber 1984). The most polyphagous of these species are from the North American *Papilio glaucus* group of Section III and the South American *Papilio scamander* group of Section V (Munroe 1961, Scriber 1988). The behavioral and physiological mechanisms by which this atypically broad feeding capability is achieved in *P. glaucus* and *P. scamander* species groups is the object of general studies in our laboratories. We are also interested in the systematic relationships of Section III and Section V species (Scriber *et al.* 1991).

It has been long recognized that the North American *glaucus* species

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group (*P. glaucus* L., *P. alexiares* Hoppfer, *P. rutulus* Lucas, *P. eurymedon* Lucas, and *P. multicaudatus* Kirby) and the *troilus* species group (*P. troilus* L., *P. pilumnus* Boisduval, and *P. palamedes* Drury) are closely related (Forbes 1951, Munroe 1961, Brower 1959a). A number of strong arguments can be made for considering these *glaucus* and *troilus* groups as sister taxa (Hancock 1983, Scriber *et al.* 1991, Hagen and Scriber 1991), and both are included in Section III. Numerous interspecific hand-pairings (within Section III, Munroe 1961) have produced viable hybrids between many taxa of both groups (Scriber 1982, 1988, Scriber *et al.* 1988[90], 1990a, Scriber and Lederhouse 1988[89], West and Clarke 1987[88]). Hancock (1983) identified 3 Central and South American species groups (*scamander*, *zagreus*, and *homerus*) comprising Section V as sister taxa to the *glaucus* and *troilus* groups. Among criteria for linking the Section III and Section V as sister taxa were the similarities in larval host families. In addition, the Rutaceae, Lauraceae, and Magnoliaceae (used by both Sections III and V) share secondary chemicals with the South American Hernandiaceae and Berberidaceae used by Section V (Scriber *et al.* 1991). Other characters linking the two sections include a "mature, solitary, smooth, green larva with metathoracic eyespots and, usually, a transverse dark band on the first abdominal segment" (Hancock, 1983). A character differentiating the two sections is an X-shaped saddle in Section V (= subgenus *Pyrrhosticta* of Hancock's classification) versus the smooth green mature larvae without the saddle in Section III (= subgenus *Pterourus* of Hancock's classification). Hancock (1983) suggested that Section V represents a South American offshoot of Section III.

In this study we produced viable hybrids between the South American *P. scamander* and *P. cleotas* (of Section V) and species of the North American Section III. We illustrate the adult and larval color patterns of resulting hybrids and report food plant utilization abilities of the hybrids.

Methods

Adults of *Papilio scamander* were collected near Campinas, Brazil in late March 1988 and brought in envelopes to East Lansing, Michigan for oviposition or hand-pairing with 1987 lab-reared virgin females of *Papilio glaucus* and *Papilio palamedes* and *P. troilus*. Larvae of *P. scamander*, collected in Campinas, Brazil from the Asian ornamental *Michelia champaca* (Magnoliaceae) used in street arborization, were also brought to Michigan for pupation. Two subsequent female *P. scamander* adults were hand paired to *P. g. glaucus* males. Hybrid adult males (*P. glaucus* × *P. scamander*) were backcrossed to virgin *P. glaucus*. Laboratory-reared males were fed a mixture of 1 part honey to 4 parts water supplemented with amino acids and electrolytes for at least 3 days prior to handpairing (Lederhouse *et al.* 1990). Field-collected and laboratory-mated females were set up in plastic boxes (10 cm x 20 cm x 27 cm) with a sprig of tuliptree, *Liriodendron tulipifera*; sweetbay, *Magnolia virginiana*; *Michelia champaca*; black cherry, *Prunus serotina*; and/or redbay, *Persea borbonia* under

saturated humidity. The boxes were placed 0.7 - 1.0 m from 100 watt incandescent bulbs under a 6 hr photoperiod followed by 6 hr of darkness. Females were fed a mixture of 1 part honey to 4 parts water at least once daily. Females were allowed to oviposit until death. Eggs were collected and counted at 2-day intervals except on weekends. Larvae were removed as they hatched, and the remaining eggs were monitored for 10 days after the last larva hatched. Egg viability was the proportion of the total eggs laid that hatched. Eggs that changed color but did not hatch were scored as fertile. Using fine camel-hair brushes, first instar larvae (neonates) were gently placed on fresh leaves of various potential host plants for bioassays of consumption and survival. Leaf moisture was maintained using aquapics, and fresh leaves were provided 3 times per week throughout larval development.

Results
PAIRINGS AND FOODPLANT USE

Table 1. Lab pairings of female *Papilio glaucus glaucus* (North American, Section III) with male *Papilio scamandar* (South American, Section V).

Mother number	Morph	Total eggs	Number of larvae	Additional fertile eggs	% fertile	% viable
5181	D	74	2	3	6.8	2.7
5182	D	191	9	3	6.3	4.7
5187	D	84	0	0	0.0	0.0
5188	D	10	0	0	0.0	0.0
5210	D	9	0	0	0.0	0.0
5939	Y	0	0	0	—	—
6226	D	1	0	0	0.0	0.0
6835	D	24	0	0	0.0	0.0
6840	D	0	0	0	—	—
6841	Y	0	0	0	—	—
6866	D	0	0	0	—	—
6868	Y	0	0	0	—	—

Twelve hand-pairings of *Papilio glaucus glaucus* females with *P. scamander* males were made. Although females from seven pairings produced some eggs, larvae were obtained from only two of the females (Table 1), plus one of two *P. glaucus* female × *P. cleotas* male pairings. The fertility and viability of the eggs were very low (less than 10%) in *P. scamander* crosses but higher (68%) in one *P. cleotas* cross. Zero fertility was observed in two additional hybrid pairings (*P. scamander* female × *P.g.glaucus* male, Fig 1a) and in two backcrosses of *P.g.glaucus* females with hybrid males (Table 2), as well as all six pairings between *scamander* or *glaucus* and Brazilian species in Section IV (*astyalus*, *anchisiades*, *torquatus*, and *hectorides*).

Of the two hybrid larvae produced in brood 5181 (*P. glaucus* × *P. scamander*), both survived the first instar and to pupation on *Magnolia*

Table 2.   Hybrid and Backcross Pairings with *Papilio glaucus* and *Papilio scamander.*

Code 5244	*P. scamander* (female)	x *P. g. glaucus* (male)	= no larvae (hybrid)
Code 5230	*P. scamander* (female)	x *P. g. glaucus* (male)	= no spermatophore (hybrid)
Code 5458	*P. g. glaucus* (female)	x *P. g. glaucus* x *P. scamander* (hybrid male from 5181)	= no spermatophore (backcross)
Code 5599	*P. g. glaucus* (female)	x *P. g. glaucus* x *P. scamander* (hybrid male from 5181)	= no spermatophore (backcross)

virginiana. The neonate larval survival of nine individuals from brood 5182 was: 100% (n=1) on *Prunus serotina* (Rosaceae), 100% (n=1) on *Liriodendron tulipifera* (Magnoliaceae), 50% (n=2) on *Magnolia acuminata* and 67% (n=3) on *Magnolia virginiana*, and 0% (n=2) on *Persea borbonia* (Lauraceae). Larvae from 5182 were reared to pupation on each of the first three plants (Table 3).

Neonate larvae of *cleotas* x*glaucus* 6210 (n=26) fed and grew very well on *Talauma ovata*, the only native Brazilian Magnoliaceae, and moderately well on the introduced *Michelia champaca*, in the same family. They rested on, but hardly fed on, *Cryptocarya aschersoniana* (Lauraceae,

Table 3.   Hybrid (*Papilio glaucus* x *P. scamander* from brood 5181 and 5182) larval survival/development on five plant species. All food plants tested except *Persea borbonia* are satisfactory hosts of *P. glaucus*. None are encountered naturally by *P. scamander*.

Foodplant Genus Species	Family	n	Survival through 1st stadia	Survival to pupation
Magnolia virginiana (sweetbay)	MAGNOLIACEAE	5	80%	Yes
Magnolia acuminata (cucumbertree)	MAGNOLIACEAE	2	50%	Yes
Liriodendron tulipfera (tuliptree)	MAGNOLIACEAE	1	100%	Yes
Prunus serotina (black cherry)	ROSACEAE	1	100%	Yes
Persea borbonia (redbay)	LAURACEAE	2	0%	No

used by both *scamander* and *cleotas* in the field). None reached the second instar.

Two pairings of *Papilio palamedes* virgin females with *P. scamander* males were made. Both of these pairings produced viable hybrids. It is noteworthy that fertility and viability of the eggs were greater than observed for the *glaucus* × *scamander* hybrids (Table 4). Of 30 hybrid larvae set up from brood 5194, first instar survival was observed as: 70% (n=10) on *Persea borbonia*; 57% (n=7) on *Cinnamomum camphora*; 25% (n=8) on *M. virginiana*, 0% (n=4) on *L. tulipifera*; and 0% (n=1) on *M. acuminata*. Hybrid survival for four larvae from brood 5198 was 33% (n=3) on *Persea borbonia* and 0% (n=1) on *M. acuminata*. The two species of Lauraceae (redbay and camphortree) supported vigorous hybrid larval growth until the final instar, but none of these large larvae were able to successfully pupate (Table 5, Fig. 2). A pairing of a *P. palamedes* male with a *P. astyalus* female (Section IV), gave only 7 eggs, none of which hatched.

Table 4. Lab pairings of female *Papilio palamedes* (North American, Section III) with male *Papilio scamandar* (South American, Section V).

Mother number	Total eggs	Number of larvae	Number of additional fertile eggs	% fertile	% viable
5194	167	31	14	26.9	18.6
5198	22	4	4	36.4	18.2

Table 5. Hybrid (*P. palamedes* x *P. scamander* from brood 5194 and 5198) larval survival/development on five plant species. Pure *P. palamedes* develop successfully on the two lauraceous host but die on the Magnoliaceae.

| Foodplant Genus Species	Family	n	Survival through 1st stadia	Survival to pupation
Magnolia virginiana (sweetbay)	MAGNOLIACEAE	8	25%	No
Magnolia acuminata (cucumbertree)	MAGNOLIACEAE	2	0%	No
Liriodendron tulipfera (tuliptree)	MAGNOLIACEAE	4	0%	No
Persea borbonia (redbay)	LAURACEAE	13	62%	Huge larvae (but unsuccessful)
Cinnamomum camphora (camphortree)	LAURACEAE	7	57%	Huge larvae (but unsuccessful)
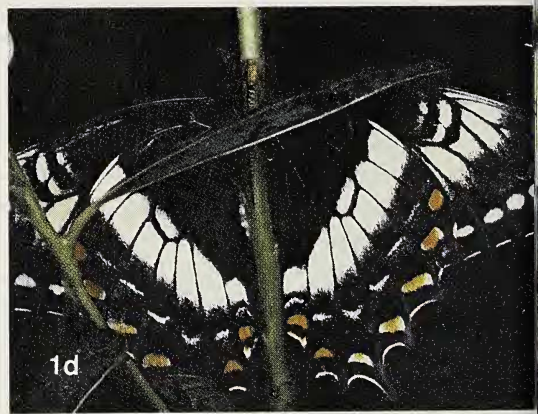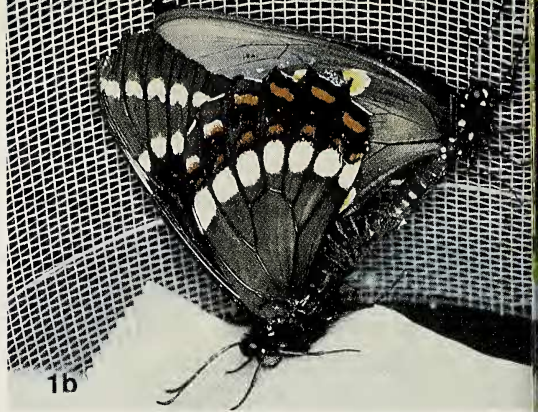
Fig. 1   a) A *Papilio scamander* female (top, from Campinas, Brazil) in copulation with a *P. g. glaucus* male (bottom, from Clinton County, Michigan, USA). b) A *Papilio troilus* female (top, from Allegan County, Michigan, USA) in copulation with a *P. scamander* male (bottom, from Campinas, Brazil). c) Dorsal view of a hybrid male adult reared on *Prunus serotina* from a hand-pairing of a dark morph *Papilio glaucus glaucus* female with a *P. scamander* male (from Campinas, Brazil). d) Ventral view of another hybrid male adult reared on *Liriodendron tulipifera* of the same pairing (#5182) as the hybrid figured in 1c. e) Dorsal view of a female hybrid adult reared on *Magnolia virginiana* from pairing (#5181). f) Ventral view of the same hybrid female adult.
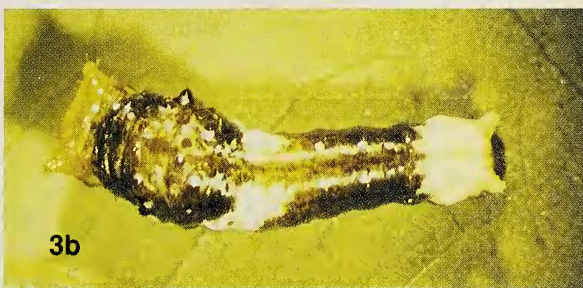
2b

2d

2f

3b

3d

3f

Table 6.   Larval survival and development of *Papilio garamas** on four plant species.

Foodplant		Family	n	Survival through 1st stadia	Survival to pupation
Genus	Species				
Magnolia virginiana (sweetbay)		MAGNOLIACEAE	2	50%	Yes
Liriodendron tulipfera (tuliptree)		MAGNOLIACEAE	4	50%	Yes
Persea borbonia (redbay)		LAURACEAE	4	75%	Yes
Sassafras albidum (sassafras)		LAURACEAE	5	80%	Yes

A virgin *Papilio troilus* female was successfully hand-paired with a *P. scamander* male (Fig. 1b). However, no eggs were obtained from this female. Two additional pairings of *P. g. glaucus* females from Michigan pupae with field-captured *P. scamander* males were made in Brazil in January, 1989. Only one infertile egg was obtained.

Papilio garamas from Mexico is another species from Section V with larvae strikingly similar to *P. scamander* and *P. cleotas* and with the ability to feed on both the Magnoliaceae and Lauraceae (Table 6). Five hand-pairings of virgin *P. g. glaucus* and *P. garamas* males were made (6228-6232). However, no eggs were obtained from these females.

Fig. 2   a) A second instar hybrid larva reared on *Magnolia acuminata* of a female *Papilio glaucus glaucus* and male *P. scamander* pairing (#5182). b) A fourth instar hybrid larva reared on *Magnolia virginiana* of a female *P. g. glaucus* × *P. scamander* pairing (#5182). c) A fifth instar hybrid larva of a *P. g. glaucus* × *P. scamander* pairing (#5181). Note the intermediate thoracic "eyes" and the intermediate mid-abdominal X-saddle compared to the parental types below (Fig. 2e, 2f). d) A prepupal hybrid of a *P. g. glaucus* × *P. scamander* pairing (#5182). e) A fifth instar *P. scamander* larva collected in Campinas, Brazil in late March, 1988. Note the abdominal X-saddle and the thoracic band of "eyes". f) A fifth instar *P. glaucus* larva. Note the smooth green body and cohesive thoracic "eye".

Fig. 3   a) A first instar hybrid larva of a *Papilio palamedes* female × *P. scamander* male pairing (#5198). b) A second instar hybrid larva of a *P. palamedes* female × *P. scamander* male pairing (#5194). c) A fourth instar hybrid larva of a *P. palamedes* × *P. scamander* pairing (#5194). d) A fifth instar hybrid larva of a *P. palamedes* × *P. scamander* pairing (#5194). e) A fifth instar *P. palamedes* larva. f) A fifth instar *P. garamas* larva (#5988).

LARVAL AND ADULT COLOR COMPARISONS

An adult hybrid (*P. g. glaucus* × *P. scamander*) male is illustrated in dorsal (Fig. 1c) and ventral view (Fig 1d). The hybrid larvae of female *P. g. glaucus* with male *P. scamander* are illustrated for the second, fourth, and fifth instar (Fig. 2a, b, c). The hybrid prepupal stage (Fig. 2d) show remnants of the *P. scamander* cross saddle (Fig. 2e), which is lacking in *P. glaucus* (Fig. 2f).

The hybrid larvae of female *P. palamedes* with male *P. scamander* are illustrated for the first (Fig. 3a) second (Fig. 3b), fourth (Fig 3c), and fifth instars. A fifth instar *P. palamedes* is shown for comparison (Fig. 3e). The fifth instar of the Mexican *P. garamas* (also of Section V) is illustrated for comparison (Fig. 3f, see also Fig 2e).

Discussion

Interpretation of the phylogenetic significance of hybrid incompatibilities is difficult (Ae 1979, Collins 1984, Lorkovic 1986, Geiger 1988, Coyne and Orr 1989). Since no clear standard of reference exists despite Ae's (1979) fine work, our evaluation must be largely descriptive. Incompatibility in presumed regulatory genes occurs predominantly at developmental stages where new groups of genes begin to interact. Our experience with *Papilio* and the literature on intergeneric crosses (Peigler 1978, Carr 1984) suggests that the genes for producing a larva remain relatively unmodified. However, genes affecting developmental stages such as pupation or adult emergence are more likely modified between species. The hybrid compatibility between species believed to be closely related, such as *Papilio troilus* and *P. palamedes* , may be quite low because of relatively small changes in key genes. This further complicates the evaluation of hybridization data.

Nevertheless, the degree of genetic compatibility of *Papilio scamander* and *P. cleotas* of the subgenus *Pyrrhosticta* (Section V) with *P. glaucus* and *P. palamedes* of the subgenus *Pterourus* (Section III) was surprising. These insect species are currently separated in distribution by about 5000 miles and by the Central American isthmus. Although these two sections are considered to be sister taxa (Munroe 1961, Hancock 1983), it is still significant that both adult males and females were obtained for *P. g. glaucus* × *P. scamander* pairings. This is remarkable since relatively few hybrid females of interspecific pairings within the *P. glaucus* species group itself are able to survive to adulthood (with the exception of *P. glaucus* × *P. alexiares* pairings; West and Clarke 1987[88], Scriber *et al.* 1988, 1990). Pairings of *P. glaucus* and *P. pilumnus* have similarly produced only male hybrid offspring (Scriber and Lederhouse 1988[89]).

The inability for any hybrids of *P. palamedes* × *P. scamander* to successfully pupate suggests a developmental incompatibility. The fertility and viability of *palamedes* × *scamander* eggs were considerably better than *glaucus* × *scamander* pairings (Tables 1 and 4). Larval growth was excellent until the final instar, although none of these healthy-looking hybrids could successfully pupate (see Figs. 3c, 3d).

Hybridization of *glaucus* with *cleotas* gave high initial juvenile viability; this needs to be repeated under more favorable conditions, perhaps on small growing plants to avoid the likely phenolic oxidation suspected in excised *Talauma ovata* leaves. The relatively high biological compatibility between Section III and Section V *Papilio* species does not support their maintenance in separate genera or even subgenera (*Pterourus, Pyrrhosticta*), though they can be conveniently separated from the species in Section IV (*Heraclides*) with which they share very low fertility and viability upon hybridization (this work and Ae, 1979).

The foodplant utilization abilities of hybrid larvae were not especially surprising since *P. scamander* feeds commonly on both the Magnoliaceae and Lauraceae (Jordan 1907, Scriber 1984, Ruszczyk 1986). The *P. troilus* species group tend to be specialized on plants of the Lauraceae, and hybrids of *palamedes* × *scamander* survived and grew very well on both redbay, *Persea borbonia*, and camphortree, *Cinnamomum camphora* (both of the Lauraceae). In contrast, the three Magnoliaceae foodplants (*Magnolia virginiana, M. acuminata,* and *Liriodendron tulipifera*) appeared to be poorer foods with no first instar survival on the latter two plant species (see Table 5).

In contrast, the *glaucus* × *scamander* hybrids survived and grew well on the three Magnoliaceae species and black cherry, *Prunus serotina* (Rosaceae), but none survived on the Lauraceae (redbay, see Table 3). It is interesting that hybrids of *P. glaucus* × *P. scamander* would initiate feeding and survive on black cherry whereas none of the hybrid larvae (n=27) of *P. glaucus* × *P. pilumnus* could do so (Scriber and Lederhouse 1988[89]). Although hybrids of *glaucus* × *pilumnus* could use all Magnoliaceae tested (Scriber and Lederhouse 1988[89]), hybrids of *palamedes* × *scamander* could use neither tuliptree nor cucumbertree of the Magnoliaceae and did poorly on sweetbay (Table 5). The *scamander* population in Campinas feeds on at least 4 genera of Lauraceae (*Persea gratissima, Ocotea corymbosa, Chrytocarya aschersoniana, Cinnamomum zeylanicum,* and two Magnoliaceae (*Michelia champaca* and *Talauma ovata*) and accepts and may regularly use an introduced Sterculiaceae, *Brachychiton* (see Ruszczyk, 1986). In southern Brazil, *cleotas* uses *T. ovata, C. aschersoniana, Persea rigida,* and *Ocotea* species, thus also combining both families in its diet.

These differential abilities support the concept that major phytochemical differences exist between the Magnoliaceae and the Lauraceae (Scriber 1986). Even within these plant families differences in feeding behavior and detoxification ability exist within certain *Papilio* taxa for different plant species (Hagen 1986, Scriber *et al.* 1991, Nitao *et al.* 1991). The fact that any North American hosts were acceptable and suitable for the *P. scamander* hybrids is intriguing. Additional studies to assess the extent of the feeding and growth capabilities of the generalized *P. glaucus* larvae on an array of South American hosts, and the reciprocal study of the South American generalist (*P. scamander*) on North American plants are planned.

Additional interspecific, intergroup, and inter-sectional pairings will help resolve the systematic and phylogenetic relationships of the various taxa in Sections III and V of the genus *Papilio* . A generally agreed upon phylogeny would greatly improve our understanding of the evolution of generalized feeding habits (e.g. upon several families of phytochemically diverse plant species) (Miller 1987b). For example, it will be interesting to know if the same general (e.g. mixed function oxidases) or specific detoxification enzymes are used by both *P. glaucus* and *P. scamander* or *cleotas* on Magnoliaceae, and similarly for *P. palamedes* and *P. scamander* or *cleotas* on the Lauraceae. The same could be said for the other Section III and Section V Lauraceae/Magnoliaceae feeders in North, South and Central America (e.g. *Papilio garamas*, Table 6).

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